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PERIODICITY IN FYNBOS OF THE NON-SEASONAL RAINFALL BELT

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Abstract

Shoot elongation, flowering and leaf fall were recorded for one representative each of the proteoid, ericoid and restioid life form of fynbos on the Outeniqua mountains near George and the lower slopes of the Swartberg, Swartberg Pass. Maximum growth for restios was in winter/spring, for proteoid species summer, whilst ericoid species grew all the year round. Maximum leaf fall for all life forms was in late summer in the Outeniquas and autumn in the Swartberg. Flowering season varied between and within life forms. Results are discussed in relation to seasonality in Californian chaparral and Australian heathland.

Uittreksel

PERIODISITEIT IN FYNBOS VANAF DIE NIE-SEISOENALE REËNSTREEK

Lootverlenging, blomtyd en blaarval is aangeteken vir een verteenwoordiger van elk van die proteoid, ericoid en restioid groeivorms van fynbos op die Outeniekwaberge naby George en laer hange van die Swartberg, Swartbergpas. Maksimum groei vir restios was gedurende winter/lente, vir proteoid species gedurende die somer, terwyl ericoid species deur die hele jaar gegroei het. Maksimum blaarval het gedurende laat somer in die Outeniekwas en herfs in die Swartberg vir alle groeivorms voorgekom. Blomseisoen het tussen en binne groeivorms gevarieer. Die resultate word bespreek in verhouding tot seisoenaliteit in Kaliforniese ,,chaparral'' en Australiese ,,heathland''.

Introduction

The diversity of plant life in any one locality is dependent on the degree to which resources are partitioned between competing populations. Temporal partitioning of resources is one aspect of niche differentiation in plant communities. Seasonality in the species rich Cape fynbos has been recorded by Kruger (1980) and Williams (1972) who noted varied phenorhythms in different life forms and within life forms.

Seasonality is not only of interest in exploring modes of competition, but also the interrelationships of plants and consumers—especially nectarivores, and the response to different fire regimes and fire seasons. Very little is known about the influence of seasonal events in fynbos on consumers. In the Swartberg, for example, nectarivores appear to be dependent on *Protea eximia* when other Proteaceae are not flowering. This species flowers throughout the year with apparent peak flowering in summer whereas most other Proteas flower from late summer to early winter. Management affecting the species would thus affect a

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number of dependent organisms. Optimal fire season is also linked to phenology since post-fire survival is partly dependent on flowering and fruiting periodicity, particularly for species with short-lived seeds lacking in fire protective devices. Jordaan (1949, 1965) observed poor regeneration of *Protea repens* (= *mellifera*) in winter burns which he ascribed to the phenological status at the time of burn. He divided fire seasons into safe, unfavourable and dangerous according to phenophase.

This note reports one year's observation on seasonal rhythms of the proteoid, ericoid and restioid life forms in the non-seasonal rainfall zone of the Outeniqua (coastal) and Swartberg (inland) mountains of the Southern Cape. It is hoped that despite the study's limitations it may stimulate greater interest in a rich and poorly explored field where the ecophysiologist, in particular, has much to offer.

STUDY AREA

Plants were studied from two localities. These were Tierkop (S 33 ° 55′ E 22 ° 31′) a hill on the Outeniquas behind Saasveld Research Station, near George, and Swartberg Pass (S 33 ° 22′ E 22 ° 6′) on the Great Swartberg Range. The Tierkop site was at an elevation of 520 m on a E.S.E. aspect of 20 % slope. The soil was a dark, acid, loamy lithosol (Mispah Form) with a relatively high organic matter content, derived from Table Mountain Sandstone. The Swartberg study area was located near the southern foot of the pass at 950 m on a southern aspect of 25 % slope. The soil was litholic (Glenrosa Form) and with a moderately deep, neutral, coarse sandy loam topsoil overlying a shallow subsoil which overlies Table Mountain Sandstone.

CLIMATE

Outeniquas: The Tierkop site on the Outeniquas has a mild temperate climate, classified as Cfb in the Köppen System (Köppen, 1931). Mean monthly temperature and rainfall at George (Weather Bureau, 1960) about 5 km from the site is summarised as a climate diagram (Walter and Lieth, 1967) in Figure 1. Mean annual temperature is 16,4 °C and precipitation is 850 mm of which 42 % falls in the winter half year. Potential evapotranspiration (P.E.T.), defined as "the water loss which will occur if at no time there is a deficiency of water in the soil for use of vegetation" (Thornthwaite, 1944), has been calculated for George using Penman's formula (ex Israelsen & Hansen, 1966). (Fig. 1). A deficit between rainfall and P.E.T. is apparent over the summer months and a moisture excess in winter. The effective moisture regime thus resembles a winter rather than a summer rainfall region. This is confirmed by streamflow records for the Kaaiman's River, the drainage of the Tierkop catchment, which has minimum runoff in December, January and February (Department of Water Affairs, unpublished records, 1960 to 1970).

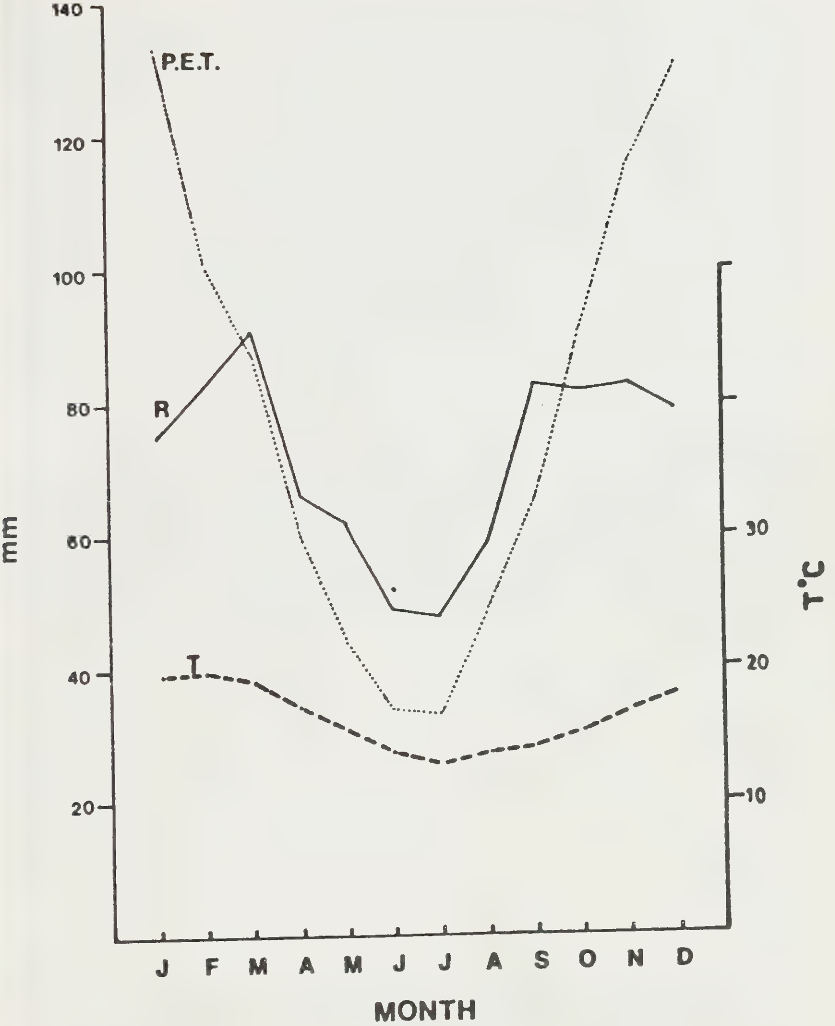


FIG. 1.
Climate diagram (Walter & Lieth, 1967), George (S 33 ° 58′, E 22 ° 25′, elevation 221 m) 1878–1950 with Penman estimates of Potential Evapotranspiration (P.E.T.).

Swartberg: The Swartberg area has a "steppe" type climate classified as BSk in the Köppen system. Climatic data from the Cango Caves station, situated about 12 km from the Swartberg site and in a similar position, are summarised in Figure 2. Mean annual temperature is 16,5 °C and precipitation (1955–1970) is 363,1 mm of which 49 % is winter rainfall (Weather Bureau, unpublished records). Inadequate data prevented calculation of P.E.T., but a similar pattern to Tierkop with maximum moisture stress in the summer months is probable. This is indirectly confirmed by Perdepoortrivier streamflow records (1965–1976) from a catchment on the southern slopes between Swartberg Pass and Cango Caves. Minimum runoff is between December and March and maximum between April and September (Department of Water Affairs, unpublished records).

Deviations from mean monthly values of rainfall and temperature of George and Cango Caves during the study period are listed in Table 1 (Weather Bureau, unpublished).

VEGETATION

Tierkop, Outeniquas

The Tierkop site was situated on a broad interfluve on the Outeniqua mountains. The vegetation was a mature 1,5–2 m high proteoid shrubland dominated by *Leucadendron uliginosum* R. Br. subsp. *uliginosum* in the upper stratum. Mid-layer shrubs were mostly *Erica seriphiifolia* Salisb. with associated *Penaea cneorum* E. Mey. A relatively dense layer of Cyperaceae (mainly *Tetraria*

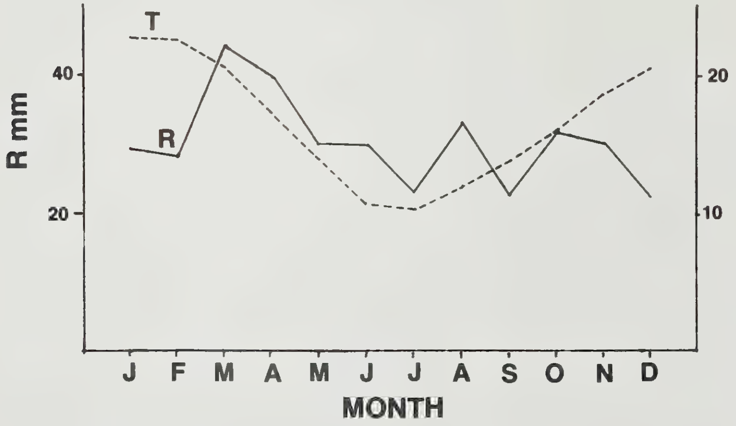


Fig. 2.
Climate diagram, Cango Caves (S 33 ° 23′, E 22 ° 13′, elevation 640 m), 1955–1970.

Table 1

Percentage deviation from monthly values of mean rainfall and temperature for George and Cango Caves over the study period, 1977–1978

Year		1978					1977								
Month		J	F	M	A	M	A	M	J	J	A	S	O	N	D
Rainfall Deviation	George	−2,8	−71,0	−37,9	−28,8		−58,6	+164,4	−56,5	−72,3	+78,8	+48,3	−41,6	+26,1	−31,1
	Cango Caves	+112,3	−78,7	−84,1	−60,8	−25,0			+77,4	−26,4	+14,3	+87,2	−0,6	+40,5	+38,4
Temperature Deviation	George	+5,4	−2,0	+7,0	+1,2		+10,8	−1,4	+5,0	+15,7	+11,8	−3,5	+7,8	+7,0	+8,6
	Cango Caves	+4,6	+2,8	−7,7	+11,7	+3,0			−5,3	−4,6	+0,9	+3,7	0,0	−0,5	−3,3

capillacea (Thunb.) C. B. Cl.) and Restionaceae (*Elegia parviflora* Kunth, *Restio triticeus* Rottb., *R. compressus* Rottb. and *E. juncea* L.) was present. The community is widespread on warmer, mid and upper elevation slopes in the Outeniqua and Tsitsikamma mountains.

Swartberg Pass

The study area was on the lower foothills, near the transition to Mountain Rhenosterveld on Nama System shales. The vegetation was a mature, 1,5 to 2,0 m proteoid shrubland dominated by *Protea repens* (L.) L. in the upper stratum associated with *P. eximia* (Knight) Fourc. *Phylica paniculata* Willd. was common in a species rich shrub layer with associated *Protea lorifolia* (Knight) Fourc., *Agathosma mundii* Cham and Schlechtend, *Stoebe* spp., *Anthospermum*, etc. Large restio tussocks occurred with frequent *Restio fruticosus* Thunb., *Cannamois dregei* Pillans, *Willdenowia teres* Thunb. and *Hypodiscus striatus* (Kunth.) Mast. Sedges and grasses, about equally represented, were of minor significance. The community is representative of relatively xeric southern slope vegetation on the Swartberg.

METHODS

Species belonging to three representative life-forms were selected at each site. These were *Leucadendron uliginosum* ssp. *uliginosum* (proteoid), *Erica seriphiifolia* (narrow-leaved, ericoid shrub), and *Elegia parviflora* (restioid) on Tierkop and *Protea repens* (proteoid), *Phylica paniculata* (narrow-leaved, ericoid shrub) and *Restio fruticosus* (restioid) at Swartberg Pass.

Four plants each of the Proteaceae and Restionaceae and three each of the ericoid shrubs were selected. Four stems on each of the shrubs were marked and four young *Restio* shoots on each restio.

Shoot elongation was measured monthly between April 1977 and April 1978 at Tierkop and June 1977 to May 1978 in the Swartberg. Bud set or development, flowering, fruiting and leaf colouring or fall were recorded for each individual, and flowering periods for other, unmarked species recorded simultaneously.

RESULTS

Growth is defined here as shoot elongation and/or leaf expansion. Seasonal growth patterns of different life forms were compared by plotting mean percentage increment over the previous months shoot length (Fig. 3a and b). Growth seasons within similar life forms were strikingly similar in the two localities despite the use of different species. The proteoid species grew over the dry summer months in both areas. *Leucadendron uliginosum* commenced growth in early October, peaked in the dry month of February and ceased in April, slightly earlier than the summer-autumn growth season for Leucadendrons recorded elsewhere (Williams, 1972; Kruger, 1980). The growth patterns of *Protea repens* resembled Kruger's

(1980) observations, but events were out of phase by two or three weeks. New shoot growth was initiated in September and October, with maximum shoot elongation between mid-November and early December. A second flush of growth was evident, peaking early in March. Differences in growth season between *Protea* and *Leucadendron/Leucospermum* noted by Kruger were not apparent but more information is required on a wider variety of species.

Kruger (1980) records a late winter to early spring growth season for most fynbos shrubs. The ericoid species had no specific growth season though growth ceased or was slowest in the autumn months of April and May in the Swartberg and was least from January to May in the Outeniquas.

The restioid life forms had a well-defined growth season from late autumn to late spring (November) with some growth until February in both. This is earlier than Kruger's 1978 generalisation of a spring to early summer growth season for winter rainfall Restionaceae.

FLOWERING

Periods of budset and development and flowering are indicated in Figure 3. The Outeniqua species flowered from spring to mid-summer. *Leucadendron uliginosum* flowered from October to early in December. This is later than most Leucadendrons of the winter rainfall area (Williams, 1972). Plant species were recorded flowering at all times of the year within the vicinity of the plot with the least flowering in autumn and early winter.

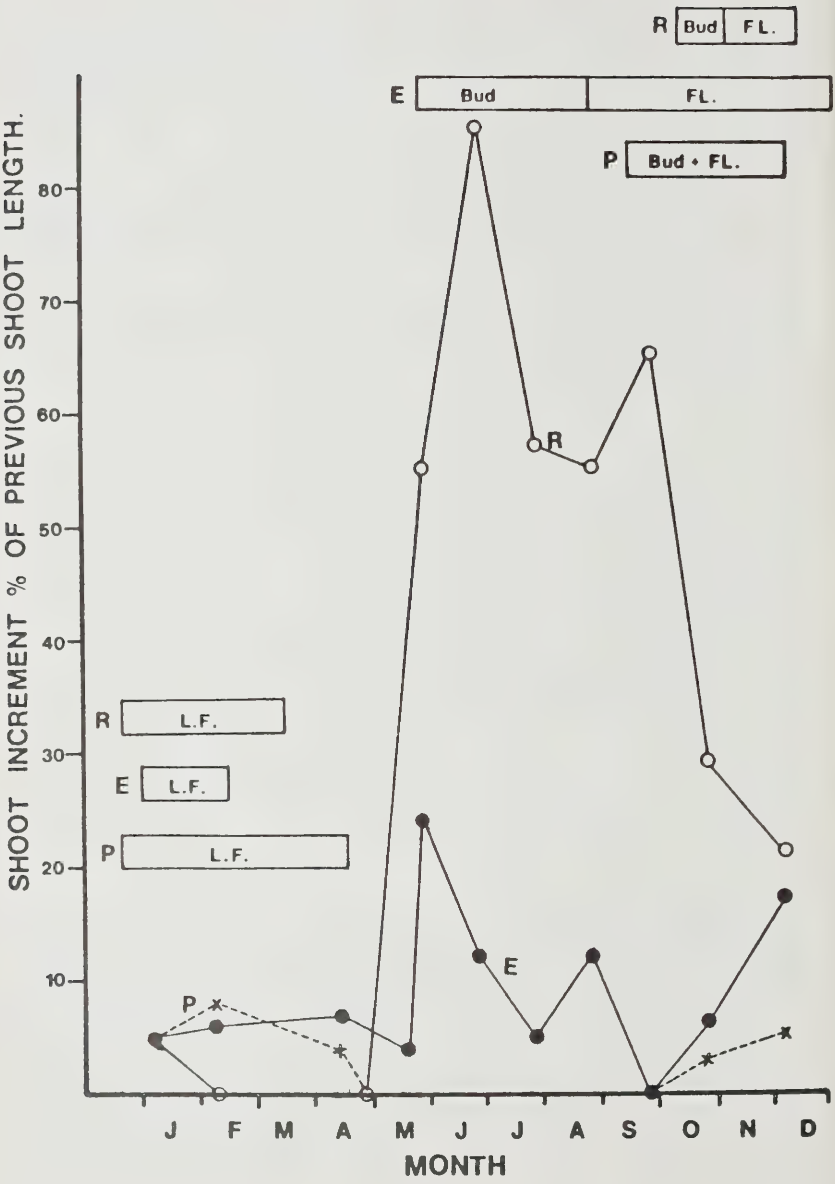
Flowering periods for the Swartberg are indicated in Figure 3b. *Protea repens* flowered from the end of February to mid-May with peak flowering in March/April. This is appreciably earlier than the May to July period (Burger, 1973 in Kruger, 1980) for *P. repens* in the Western Cape. Both the restioid *(R. fruticosus)* and ericoid *(Phylica paniculata)* growth forms flowered about two months later than their analogues on the Outeniquas, but, as in the Outeniquas, some species in the vicinity were present in flower throughout the year.

LEAF-FALL

Period of leaf-fall or partial stem die-back (in the case of Restionaceae) are indicated in Figure 3. Leaf-fall was comparatively synchronised for all the life forms studied. Kruger (1980) reported a principal leaf-fall period in late summer to autumn for Western Cape species to which the Swartberg data conforms. In the Outeniquas, however, leaf-fall was earlier being mainly mid- to late-summer.

DISCUSSION

This report describes observations over a limited period and for a limited number of species. More extended observations over a greater geographical range are required, together with studies of the relationship between stem elongation and


R Bud FL.
E Bud FL.
P Bud + FL.
R L.F.
E L.F.
P L.F.
R
E
P
SHOOT INCREMENT % OF PREVIOUS SHOOT LENGTH.
80
70
60
50
40
30
20
10
J F M A M J J A S O N D
MONTH

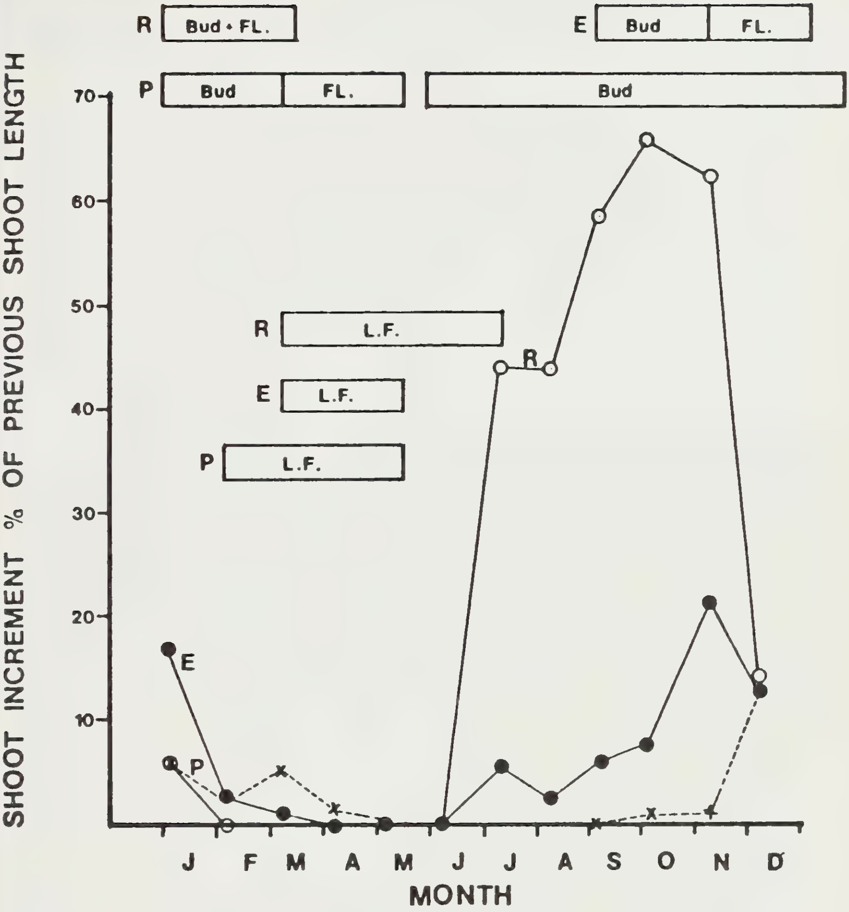


FIG. 3.

Shoot elongation as mean percentage increment over shoot length at the preceding measurement. Measurement intervals were approximately one month. Life forms and species are, for (a) R = *Elegia parviflora*, E = *Erica seriphiifolia*, P = *Leucadendron uliginosum*, and for (b) R = *Restio fruticosus*, E = *Phylica paniculata*, P = *Protea repens*. Periods of bud development (BUD), flowering (FL) and leaf-fall (L.F.) are indicated for each species. 3(a) Outeniquas, 3(b) Swartberg.

carbon gain and water loss. Nevertheless some interesting points arise. Growth periodicities are adaptations to seasonal stress on plant growth. Probable seasonal limitations on plant growth in the study area are:

Winter: Light (short photoperiod), low temperature. Water supply is more than sufficient.

Spring: Light is adequate (medium length photoperiod), temperatures are moderate, water supply is adequate. Apparently optimum conditions for growth.

Summer: Long photoperiods and warm temperatures are suitable for growth. Soil moisture deficit strongly limiting particularly as season progresses.

Autumn: Similar to spring but with a marked soil moisture deficit initially and gradual recharge towards winter.

It seems probable that nutrient availability will vary with season due to seasonal variations in litterfall and the effects of climate on decomposition (Schaefer, 1973) and that this may also affect growth periodicity. This sequence is characteristic of ecosystems with a Mediterranean climate. In California, *Heteromeles arbutifolia*, a sclerophyll shrub, is strongly limited by moisture in summer, with short photoperiod limiting in winter and temperature of minor significance in seasonal control of carbon gain (Mooney & Harrison, 1975). The dominant life form (in Californian chaparral), an ever-green sclerophyll, deep-rooted shrub, is adapted to carbon gain whenever favourable conditions of light, moisture or temperature coincide. It tolerates drought and cool winter temperatures (Morrow & Mooney, 1974). Growth periodicity tends to be bimodal with spring as the main growth season. Seasonal growth in the more humid communities of Australian sclerophyll, is confined to spring and summer. This is out of phase with the climate and has led to the suggestion of a tropical origin of the flora and its comparatively recent confinement to a Mediterranean climate (Specht, 1975).

The Cape fynbos seems to be unique for its variety of different life forms and for the range of growth periodicities adopted.

The Restionaceae in this study are unusual in opting for a growth period commencing in early winter in low temperature–low light conditions. By spring, when optimal conditions prevail, young shoots are well established and vigorous. Winter drought towards the summer rainfall areas would severely limit the distribution of these species and reduce their competitive advantage.

The two ericoid shrubs (particularly *Erica seriphiifolia*) have adopted a generalist strategy (cf. Morrow & Mooney, 1974) growing at any period when the combination of soil moisture, temperature and photoperiod is suitable. They thus resemble chaparral shrubs in growth periodicity. *Phylica paniculata*, in the Swartberg, showed a distinct peak in spring to mid-summer with limited growth in winter or autumn perhaps as a consequence of greater moisture and temperature stress in the drier climate and colder winters.

The Proteaceae grow in the driest period of the year, resembling dominant shrubs in Australian heath and mallee (Specht and Brouwer, 1975). This summer growth season would be better suited to summer rainfall areas and adds weight to the argument of a tropical or sub-tropical origin for the family (Rourke, 1972, for *Leucospermum*; Johnson & Briggs, 1975).

Phenology is probably implicated in community diversity. From the limited evidence available, the specialised summer growth strategy appears to have few adherents and the difficulties of growth in the season of maximum moisture stress is perhaps reflected in the low number of species in any community occupying the proteoid niche. In contrast the all year growth capabilities of ericoid and narrow sclerophyll shrubs would seem sufficiently flexible to allow subtle seasonal division of resources between species and thus a large number of species within the life form. Comparative studies of species within a life form, and the relative proportion of life forms with different growth periodicities along moisture/temperature/photoperiod gradients would provide further clues to the role of phenology in allowing many species to grow together in a structurally simple vegetation type.

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